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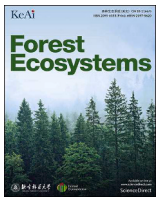

Original Article

Mixing non-native Douglas fir with native tree species is not enough to avoid negative impacts on overwintering birds

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ABSTRACT

Forest conversion toward climate-resilient non-native tree species is increasingly promoted in temperate Europe, yet biodiversity responses outside the main growing season remain poorly studied. In particular, winter conditions may constrain the biodiversity of forest organisms through reduced resource availability and harsh microclimate conditions, potentially amplifying effects of tree species composition on habitat use and community composition.

Here, we investigated how winter bird communities respond to forest stand composition by comparing pure and mixed stands of European beech, Norway spruce, and non-native Douglas fir across 38 forest plots in northwest Germany. Using passive acoustic monitoring, we quantified bird taxonomic and functional diversity from 4476 h of recordings comprising 1,816,452 total detections.

Beech-Douglas fir mixtures generally supported lower activity days, taxonomic, and functional diversity than native monocultures. Bird community composition differed consistently among stand types, with pronounced contrasts between beech- and conifer-dominated stands. In addition to stand composition, winter bird activity and diversity were strongly modulated by microclimatic conditions and vertical forest structure.

Our results, compared to previous studies conducted during the growing season, clearly show that the effects of non-native Douglas fir on biodiversity under extreme environmental conditions, i.e., in winter, cannot be deduced from findings in the summer season. Therefore, focusing solely on the main growing season carries the risk of incomplete conclusions about the consequences of forest conversion with non-native tree species for the activity and diversity of forest-associated organisms.

1. Introduction

Balancing timber production with environmental protection remains a major challenge (Gustafsson et al., 2020), as land-use intensification, resource exploitation, and climate change continue to drive biodiversity loss and undermine ecosystem stability (Hald-Mortensen, 2023). Climate-adaptive forestry addresses these pressures by promoting tree species and forest stand compositions that maintain productivity while increasing tolerance to drought and climatic stress (Temperli et al., 2012). Yet, the consequences of such strategies for biodiversity and ecosystem functioning remain uncertain, particularly when adaptation involves non-native tree species.

In temperate Europe, a prominent adaptation strategy is to replace or complement Norway spruce (*Picea abies* (L.) H. Karst.) with non-native Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Nicolescu et al., 2023). While Norway spruce is increasingly vulnerable to drought and bark beetle outbreaks outside its natural range (Löf et al., 2023), Douglas fir is valued for its relatively high drought tolerance and productivity (Thomas et al., 2022). Although its cover in Germany is currently relatively small (261,000 ha; 2.4%; BMEL, 2024), it reaches

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higher regional shares in some federal states (e.g., 7% in Rheinland-Pfalz; Landesforsten Rheinland-Pfalz, 2024; 4.3% in Hessen; PEFC Hessen, 2025), reflecting its growing role in climate-adaptive forestry. However, empirical evidence on its ecological consequences in European forests remains limited, with negative effects on biodiversity and ecosystem functioning relative to native tree species reported in some (Finch and Szumelda, 2007; Schuldt et al., 2022; Tallamy et al., 2021) but not all studies (Graf et al., 2025). To mitigate potentially negative ecological effects, its use is often recommended in mixtures with native species such as European beech (*Fagus sylvatica* L.), with admixture commonly limited to around 20% (FSC Deutschland, 2025), rather than in monocultures (Thurm and Pretzsch, 2016; Wildermuth et al., 2023). Mixed forest stands can increase the taxonomic and functional diversity of forest-associated organisms (Messier et al., 2022) and may outperform mosaics of monocultures at larger spatial scales in supporting regional species diversity (Schuldt et al., 2022) through higher species turnover between local communities (Leidinger et al., 2021). However, these benefits depend strongly on tree identity, as species differ in structural properties, resource supply, and their effects on the forest microclimate (Díaz-Calafat et al., 2023; Kovács et al., 2017; Renner et al., 2012). Because these forest features vary across the year, forest stand type effects on biodiversity may differ between seasons, with consequences for community composition and activity of forest-associated organisms (Michielsen et al., 2024).

Winter in temperate forests represents a distinct ecological context from the main growing or breeding season and can intensify environmental filtering: food availability declines, thermoregulatory costs increase, and energetic constraints can shape short-term survival with carry-over effects on subsequent reproduction success (Ingle et al., 2020; Robb et al., 2008). Birds are well suited for investigating such season-dependent responses because of their well-documented phenological patterns and sensitivity to environmental variation (Kawamura et al., 2019). Temperate-forest winter assemblages differ substantially from breeding communities, with seasonal redistribution of migrants and shifts in habitat use by resident species (Felgentreff et al., 2026; Michielsen et al., 2024). During the breeding season, bird species richness and abundance generally increase with the proportion of deciduous trees (Felton et al., 2021), whereas Douglas fir monocultures tend to support fewer species and individuals (Schuldt et al., 2022). Winter bird communities are comparatively understudied, despite evidence for seasonal shifts in species-habitat associations (Yabuhara et al., 2019), partly because detectability and vocal activity decline outside the breeding season, complicating standardized surveys (Ralph et al., 1995). Passive acoustic monitoring (PAM) with automated sound recorders can help address this limitation by enabling standardized, non-invasive sampling over extended periods (Darras et al., 2019; Knight et al., 2025; Shaw et al., 2021). Outside the breeding season, reduced territoriality and increased mobility may also weaken associations with specific stand types, and habitat use may become more responsive to local resource availability and shelter conditions (Lenz et al., 2015).

In winter, stand composition can influence resident bird activity by altering both energy intake (e.g., food availability) and energy expenditure (e.g., thermoregulatory costs; Carrascal et al., 2012). Broadleaved stands can provide energy-rich mast (Renner et al., 2012) and sun-exposed microhabitats after leaf fall (Carr and Lima, 2014; Villén-Pérez et al., 2014), whereas evergreen conifer canopies may reduce heat loss under cold and windy conditions (Díaz-Calafat et al., 2023). Tree species may also differ in their availability of winter arthropod prey, with previous work reporting lower canopy arthropod densities in Douglas fir than in Norway spruce (Gossner and Utschick, 2004). Mixed stands may moderate winter energetic constraints by providing complementary food and shelter resources at fine spatial scales (Catfolis et al., 2023; Messier et al., 2022). This may be particularly evident when going beyond taxonomic diversity. Functional diversity—the range of traits influencing resource use, energy flow, and community resilience—can provide deeper insight into ecosystem functioning and stability (Petchey and Gaston, 2006). Trait-based approaches may be especially informative in winter, when cold conditions and food limitation can favor specific trait combinations related to diet, body size, and foraging strategies (Bühler et al., 2023; Wilman et al., 2014). As arthropods become scarce, many birds rely more on plant-based foods and adjust foraging behavior and substrates, potentially constraining guilds with limited dietary flexibility, such as specialist insectivores (Renner et al., 2012).

Here, we investigated how winter bird activity, diversity, and community composition vary with tree-species composition in 38 forest plots across eight sites in northwest Germany. We compared monocultures and mixtures of Douglas fir (non-native), Norway spruce (native but planted outside its natural range), and European beech (native). Using PAM, we assessed both taxonomic (TD) and functional diversity (FD) continuously over three winter months, from December to February. We hypothesized that (i) stand-type differences in winter TD are overall weak, reflecting reduced territoriality and more flexible space use during this season; (ii) winter bird activity days and FD still differ among stand types, with Douglas fir monocultures underperforming compared to the other stand types and mixtures outperforming the corresponding conifer monoculture due to complementary resource supply; (iii) positive mixture effects become more pronounced from the local (plot) to the landscape (regional) spatial scale through greater species turnover among plots compared to monocultures; and (iv) local stand-type differences in bird species composition are only weakly pronounced because many birds form mobile flocks to track variable food and shelter across multiple stand types.

2. Materials and methods

2.1. Study design and study area

The study was conducted at eight study sites distributed across Lower Saxony, Germany (Fig. 1). The region has a temperate climate with a mean winter temperature of 2.6 °C and mean winter precipitation of 196 mm (1996–2025; German Weather Service, 2025). Each study site comprised five plots representing different stand types: (1) pure Douglas fir (stand age range: 48–76 years), (2) mixture of European beech and Douglas fir (stand age range: 66–133 years), (3) pure European beech (stand age range: 84–136 years), (4) mixture of European beech and Norway spruce (stand age range: 73–128 years), and (5) pure Norway spruce (stand age range: 60–117 years). Two plots at site 1, located in the Harz National Park, were excluded due to forest dieback, resulting in a total of 38 plots (Fig. 1). Plots covered an area of 2500 m^2, with a mean distance between plots within a study site of 1524 m (±1016 m SD).

2.2. Bird survey and data processing

Birds were surveyed using automated sound recorders (AudioMoth v1.1.0; Hill et al., 2018) from mid-November 2024 to the end of February 2025. One recorder was mounted per plot at the plot center, 1.5 m above ground on an unobstructed trunk (≥2 m radius clearance), facing east. Recorders sampled for 30 s every 10 min, both day and night (32 kHz; medium gain), following high-temporal-resolution PAM protocols (Singer et al., 2026).

Audio files were first processed with BirdNET v2.4 (Kahl et al., 2021) to detect and classify vocalizations to species level. We used a 2 s overlap to optimize the detection of single calls in winter (Pérez-Granados et al., 2025) and deactivated the eBird filter to avoid unverified exclusions of species (Sullivan et al., 2009). Species not expected to occur within the study sites during the winter, based on distribution range, migratory status, or habitat preferences, were excluded (Bauer et al., 2005), resulting in 74 species. To minimize false positives, we applied species-specific confidence score thresholds derived from manual validation of a stratified random sample of detections (10 detections per

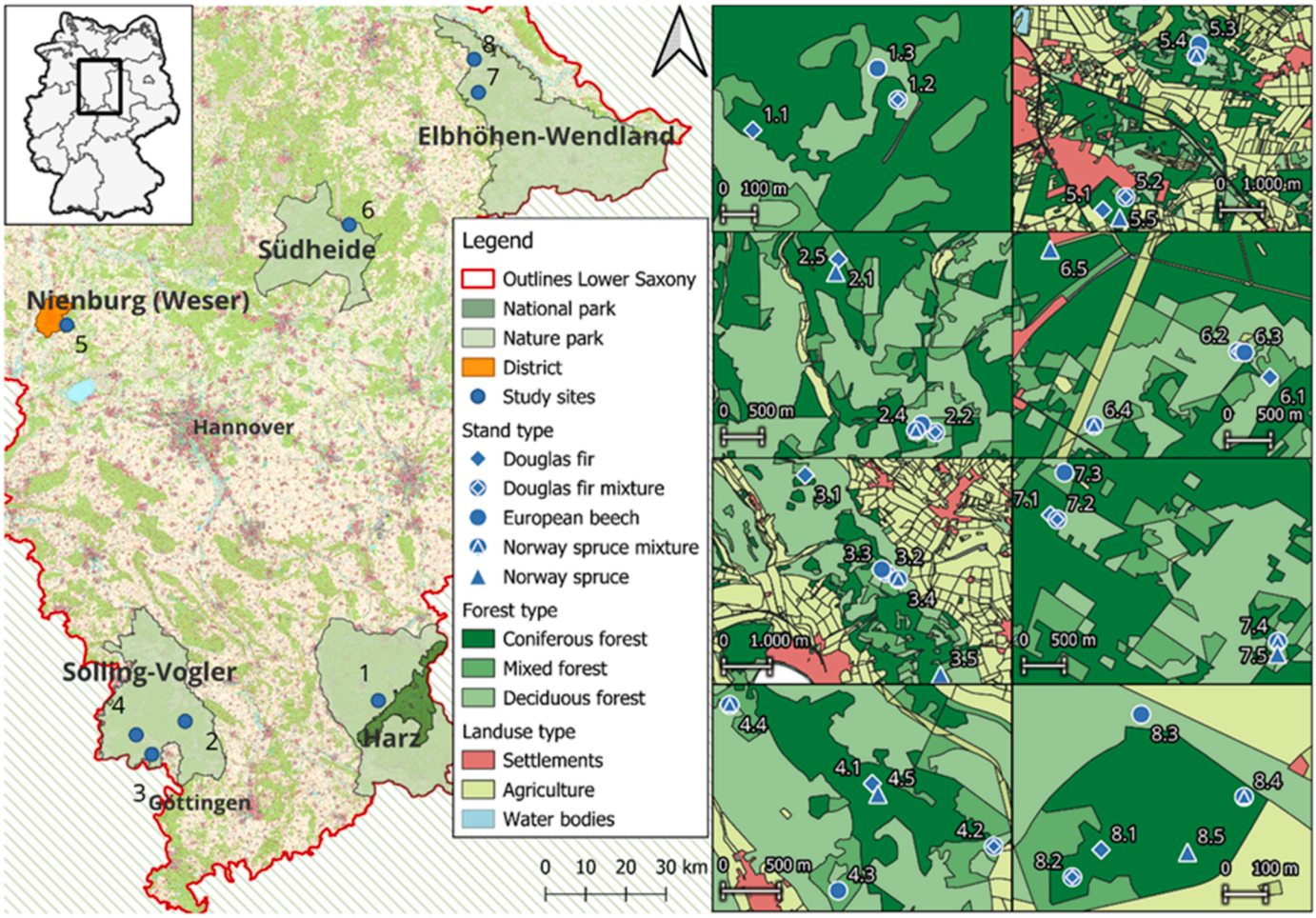

Fig. 1. Location of the study sites (on the left) and plots (on the right) in Lower Saxony, Germany. The inset map (upper left) shows the outline of Germany with the location of Lower Saxony highlighted. National and nature parks are displayed on the left, and forest and land-use type on the right. The first number of the plot label indicates the site, and the second number represents the stand type illustrated by different symbols. The map is based on DTK25 (LGLN, 2023), Basis-DLM (LGLN, 2023), VG250 (BKG, 2023), and Nationalparks and Natureparks (NLWKN, 2024).

species per 0.1 class of confidence scores; Singer et al., 2024) and logistic regression models (Wood and Kahl, 2024). Thresholds were selected based on both probability estimates and precision values, aiming to maximize reliability while retaining sufficient data. For species with limited sample sizes, lower thresholds were accepted when detections were confirmed on at least five days. Following Pérez-Granados et al. (2025), thresholds corresponding to predicted probabilities < 0.5 were excluded to ensure robustness in community-level analyses. Full validation and thresholding procedures are described in Supplementary Material.

For activity days, modelling and community composition analysis, we excluded three plots (two Douglas fir stands and one beech stand) because recording gaps exceeded 15 consecutive days, indicating insufficient and non-comparable sampling effort (Fig. S1). For TD and FD analysis, one Douglas fir plot was excluded due to markedly lower sample coverage ($SC = 0.90$) relative to the other plots (average $SC = 0.99$), to ensure robust and comparable diversity estimates across stand types.

2.3. Functional traits

For the assessment of functional diversity, we included body mass as a proxy for individual energy demand, bill length and diet (carnivore, granivore, insectivore, and omnivore) as proxies for food choice and resource type utilization, migratory status for permanent and temporal local habitat use, and feeding stratum for vertical habitat use (Bregman et al., 2016; Schuldt et al., 2022; Table S1). A species was considered migratory if its breeding range did not overlap with the study sites. Functional trait data were obtained from Bauer et al. (2005) , del Delgado and Penteriani (2004), Renner and van Hoesel (2017), and Schubert (1997). Feeding stratum use (percentages across strata) was extracted from Wilman et al. (2014) and condensed into a mean foraging height index. We grouped strata into ground, mid-story (understory + mid-height), and canopy (canopy + aerial), assigned scores 1–3, and calculated a weighted mean as $(1 \times \%_{ground} + 2 \times \%_{mid\text{-}story} + 3 \times \%_{canopy})/100$.

2.4. Environmental variables

To assess the influence of environmental and structural plot characteristics on bird diversity, we measured 20 variables based on their known importance for bird assemblages (Basile et al., 2021; Carrascal et al., 2012; Shaw et al., 2024): latitude, altitude, mean stand age, mean tree diameter at breast height (DBH), variability in tree diameter calculated as the coefficient of variation (CV), mean, maximum, minimum, and CV of temperature and relative humidity during the sampling period, box dimension, mean and CV of effective number of layers ($ENL_{dim} = 0$, $ENL_{dim} = 1$, $ENL_{dim} = 2$), mean and CV of the vertical distribution ratio (VDR), mean and CV of canopy height, canopy cover, taxonomic tree neighborhood diversity (NDiv), deadwood, and the

proportions of beech, Douglas fir, and Norway spruce, as well as total forested area within a 400-m radius around the plot. For more detailed information about the environmental and forest structure variables used, see Table S2.

2.5. Statistical analysis

All statistical analyses were performed in R version 4.3.2 (R Core Team, 2023). To reduce bias from highly vocalising species, detections were aggregated to daily occurrence (i.e., activity days: each species counted at most once per day per plot; Symes et al., 2022). TD and FD were estimated with iNEXT.3D (Chao et al., 2021) at the local (plot) scale and at the landscape (regional) scale by pooling plots of the same stand type across sites. This approach implemented a unified framework for diversity estimation based on Hill numbers (Hill, 1973) and quantifies TD as the effective number of equally abundant species, and FD as the effective number of equally distinct functional groups. The order q controls sensitivity to relative abundances: $q = 0$ corresponds to species, and functional group richness (with focus on rare species), $q = 1$ to exponential Shannon diversity (with focus on common species), and $q = 2$ to inverse Simpson diversity (with focus on dominant species). To ensure comparability across samples, we standardized all diversity estimates to a sample coverage equal to the minimum coverage at double sample size (i.e., 98%; Chao et al., 2014). Functional diversity was computed from a Gower trait distance matrix (Gower, 1971) using the five traits described above (vegan package; Oksanen et al., 2025). We tested for correlations between the Hill numbers to assess redundancy among the different diversity indices using Pearson's correlation test. Plot-level TD and FD for Hill numbers $q = 1$ and $q = 2$ were highly correlated ($r = 0.99$), therefore TD and FD for $q = 2$ were excluded from further analysis (Table S4). Lastly, we quantified activity days, and species richness for each feeding guild using functions from the vegan package (Oksanen et al., 2025).

We modelled bird activity days, TD and FD, and feeding-guild-specific activity days and species richness as separate response variables using linear mixed-effects models (lme function from nlme package; Pinheiro et al., 2025) in a two-step modelling approach to independently assess the influence of stand type (stand type as fixed effect), and environmental and forest structural variables together with location (a factor discriminating northern vs southern sites) as fixed effects. To minimize multicollinearity, we screened Pearson correlations (Fig. S2) and computed variance inflation factors (VIFs) of the initial models (car package; Fox and Weisberg, 2019), and removed correlated variables with VIF > 3.5 (Dormann et al., 2013), such that the initial models contained mean age, mean temperature, box dimension, effective number of layers ($ENL_{dim} = 2$), canopy cover, tree neighborhood diversity (NDiv), deadwood, forest cover (400 m radius), and European beech and Douglas fir proportions (400 m radius) as predictors. We used the Akaike information criterion corrected for small sample sizes (AICc) (Burnham et al., 2011) under maximum-likelihood estimation (MLE). For the final model fitting, restricted maximum-likelihood (REML) was used to obtain unbiased estimates of variance components. Pairwise differences among stand types were assessed with Tukey honestly significant difference (HSD) post-hoc tests using Holm correction for multiple comparisons (Hothorn et al., 2008). To account for spatial autocorrelation, all models included study plot nested within study site as a random effect. We visually checked the model residuals for homoscedasticity and normality. We also tested whether plot-level environmental characteristics differed among stand types using linear mixed-effects models, with each plot characteristic as the response variable, stand type as a fixed effect, and site included as a random intercept. Pairwise differences among stand types were evaluated with Tukey post hoc comparisons, applying a Holm correction for multiple testing.

To test whether FD differed from expectations given TD, we compared observed FD with values from 999 randomized communities generated under Hardy's (2008) 1s null model and calculated standardized effect sizes (FD.ses; Gotelli and Rohde, 2002) as $SES = (Value_{obs} - \mu_{null})/\sigma_{null}$, where $Value_{obs}$ is the observed FD, and μ_{null} and σ_{null} are the mean and standard deviation of the corresponding null model distribution.

To estimate bird TD and FD at the landscape scale, we applied an incidence frequency-based rarefaction and extrapolation approach using the iNEXT.3D package (Chao et al., 2021). To compare gamma diversity between monocultures and mixtures, we pooled the data of three pure stand types and two mixed stand types, respectively, and repeated the same analysis for this aggregated dataset. Significant differences in extrapolated diversity estimates were inferred by non-overlapping 95% confidence intervals, following Schenker and Gentleman (2001).

Community composition was analysed using two-dimensional nonmetric multidimensional scaling (NMDS) ordination based on relative activity days and Morisita-Horn dissimilarity (vegan; Oksanen et al., 2025). Differences among stand types were tested with PERMANOVA (999 permutations), followed by pairwiseAdonis2 for post hoc comparisons (Martinez Arbizu, 2020). Homogeneity of multivariate dispersion was tested using the betadisper function (vegan; Oksanen et al., 2025). Environmental variables were fitted post hoc using envfit, and predictor effects were quantified using distance-based redundancy analysis (dbRDA) based on Horn distances. Variables were screened for collinearity (VIF < 3.9) prior to analysis, and backward stepwise model selection was performed using the "dbrda" and "ordistep" functions (vegan; Oksanen et al., 2025).

To assess whether the results on activity, diversity, and species composition were disproportionately influenced by the most acoustically active taxon, we conducted a sensitivity analysis excluding *Regulus* sp. detections.

3. Results

Over the entire survey period, we recorded a total of 537,114 audio files (4476 h) and identified 1,816,452 detections belonging to 241 species. After filtering for species present in winter in Germany, a list of 74 species was selected. During the threshold modelling and selection steps, another 35 species were excluded due to an insufficient number of true positives (<5; 27 species) or because the distribution of the detections along the confidence score range precluded the selection of a threshold (8 species), resulting in a reduced set of 39 species comprising 98,684 detections (Table S3). Detections assigned to *Regulus* sp. included Common Firecrest (*Regulus ignicapilla*) and Goldcrest (*Regulus regulus*), and *Corvus cornix* detections were added to *Corvus corone*, whose calls are difficult to distinguish reliably, resulting in a final set of 37 species. With 41,438 detections, *Regulus* sp. represented the most abundant taxon and accounted for approximately 42% of all detections included in the analysis. *Parus major* and *Dendrocopos major* were the second and third most active species, with 9032 (9%) and 7769 (8%) detections respectively.

3.1. Bird activity and diversity at plot scale

Vocal activity differed among stand types ($F_{4,23} = 5.30$, $p < 0.05$; Fig. 2a and Table S5), with significantly higher values in beech and beech-Norway spruce mixtures compared to beech-Douglas fir mixtures (beech vs beech-Douglas: estimated difference $\pm$ SE $= 380.7 \pm 103$, beech vs. beech-Douglas fir: estimated difference $\pm$ SE $= 403.5 \pm 104$, $p < 0.005$; Fig. 2a). Stand types did not differ significantly in TD for $q = 0$ ($F_{4,25} = 2.47$, $p = 0.07$; Fig. 2b). For $q = 1$, the effective number of common species was higher in beech-Norway spruce mixtures than beech-Douglas fir mixtures (estimated difference $\pm$ SE $= 3.74 \pm 1.27$, $p < 0.05$; Fig. 2c). Functional diversity did not differ among stand types for $q = 0$ ($F_{4,25} = 2.04$, $p = 0.1$; Fig. 2d). For $q = 1$, FD differed marginally among stand types ($F_{4,25} = 2.74$, $p = 0.05$; Fig. 2e and Table S6). Analyses based on standardized effect sizes of FD (FD.ses) relative to the

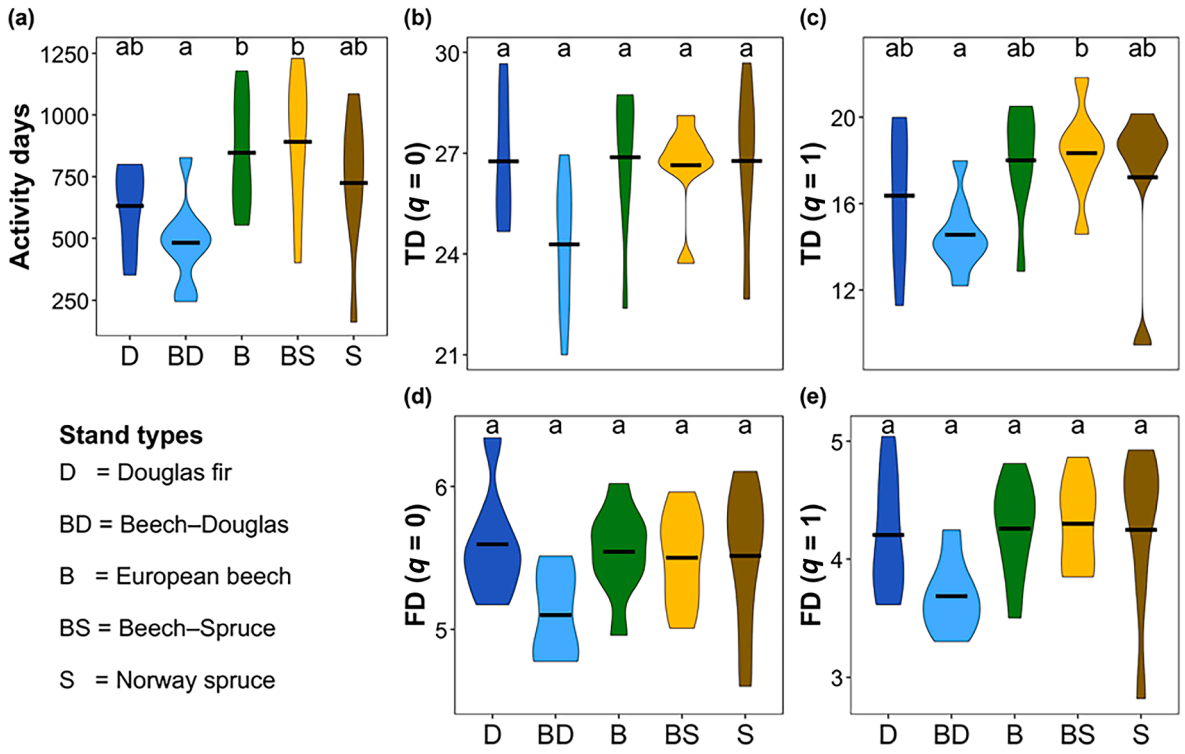

Fig. 2. Bird activity and diversity metrics calculated at the plot level ($n = 35$ for activity days; $n = 37$ for TD and FD). **(a)** Metrics include activity days, taxonomic richness for **(b)** $q = 0$, and **(c)** $q = 1$, functional richness for **(d)** $q = 0$, and **(e)** $q = 1$. Letters above violins indicate significant differences based on linear mixed-effects models followed by post-hoc pairwise comparisons ($p < 0.05$). Coloured areas reflect the data distribution. Black lines are the mean values per plot.

null model yielded qualitatively similar results across stand types, although the standardized effects were generally weaker (Fig. S3).

Carnivorous and granivorous birds showed significant differences among stand types in both activity days and richness (Fig. 3a–d and Table S7). In particular, activity days of carnivores and granivores were higher in beech (carnivores estimated difference±SE = 40.6 ± 9.75, $p < 0.001$; granivores estimated difference ± SE = 132 ± 40.2, $p = 0.009$) and beech-Norway spruce (carnivores estimated difference ± SE = 35.6 ± 9.76, $p = 0.002$; granivores estimated difference ± SE = 162 ± 40.3, $p < 0.001$) stands than in beech-Douglas fir mixtures (Fig. 3a and c). Carnivorous species richness was higher in beech stands (estimated difference ± SE = 1.3 ± 0.45, $p = 0.03$; Fig. 3b), and granivorous species richness in beech (estimated difference ± SE = 2.04 ± 0.64, $p = 0.01$) and beech-Norway spruce (estimated difference ± SE = 1.9 ± 0.64, $p = 0.03$) stands than in beech-Douglas fir mixtures (Fig. 3d and Table S7). Insectivorous bird activity days showed marginally significant differences among stand types (Fig. 3e; $F_{4,23} = 2.48$, $p = 0.07$), but species richness was significantly lower in beech-Douglas fir mixtures than in the other stand types (Fig. 3f and Table S7). Omnivorous activity days were significantly higher in beech monocultures and beech-Norway spruce mixtures compared to Douglas fir monocultures (B vs. D: estimated difference ± SE = 171 ± 56.2, $p = 0.02$; BS vs. D: estimated difference ± SE = 155 ± 55.4, $p = 0.03$) and beech-Douglas fir mixtures (B vs. BD: estimated difference ± SE = 187 ± 51.5, $p = 0.003$; BS vs. BD: estimated difference ± SE = 171 ± 51.6, $p = 0.007$; Fig. 3g), whereas omnivorous species richness differed weakly among forest stands ($F_{4,23} = 2.28$, $p = 0.09$; Fig. 3h and Table S8).

3.2. Effects of forest structure and environment on bird activity and diversity

Bird activity and diversity metrics were associated with several forest-structure and environmental variables (Fig. 4 and Table S9). Mean temperature was positively associated with all diversity metrics, with estimated slopes ranging from 0.22 ± 0.11 for FD at $q = 0$ to 234.37 ± 73.75 for activity days (Fig. 4 and Table S9). By contrast, tree-neighborhood diversity was negatively associated with TD and FD, with estimated slopes ranging from −0.87 ± 0.39 to −5.76 ± 2.41 (Fig. 4 and Table S9). For TD at $q = 1$, canopy cover had a negative association (estimate ± SE = −46.61 ± 15.79), whereas the effective number of layers ($ENL_{dim} = 2$; estimate ± SE = 2.05 ± 0.81) and beech cover within a 400 m radius around the plot (estimate ± SE = 1.62 ± 0.53) had positive associations. Functional diversity at $q = 1$ increased with the effective number of layers (estimate ± SE = 0.35 ± 0.15) and showed a weak negative association with box dimension (estimate ± SE = −3.82 ± 1.89, $p = 0.055$; Fig. 4).

Forest structure and environmental characteristics were in part related to stand type. Tree neighborhood diversity differed significantly among stand types, with mixtures showing the highest values and beech monocultures the lowest (Table S10). Stand age was significantly higher in beech and both mixtures than in Douglas fir stands. Canopy cover also differed among stand types, with Norway spruce stands showing lower canopy cover than the other stands (Table S10). European beech cover within a 400-m of the plot was highest around beech-Norway spruce mixtures and beech monocultures and lowest around Douglas fir and Norway spruce monocultures. Of the environmental and forest-structure variables tested, mean temperature, effective number of layers, and box dimension did not differ significantly among the five stand types (Table S10).

3.3. Bird diversity at landscape scale

Species rarefaction and extrapolation curves at the landscape scale (pooled across plots and sites) indicated broadly similar TD among stand types and between monocultures and mixtures for species richness ($q = 0$) (Fig. 5a and S4a). By contrast, FD at $q = 0$ showed clearer separation among stand types (Fig. 5d). In particular, FD at $q = 0$ was lowest

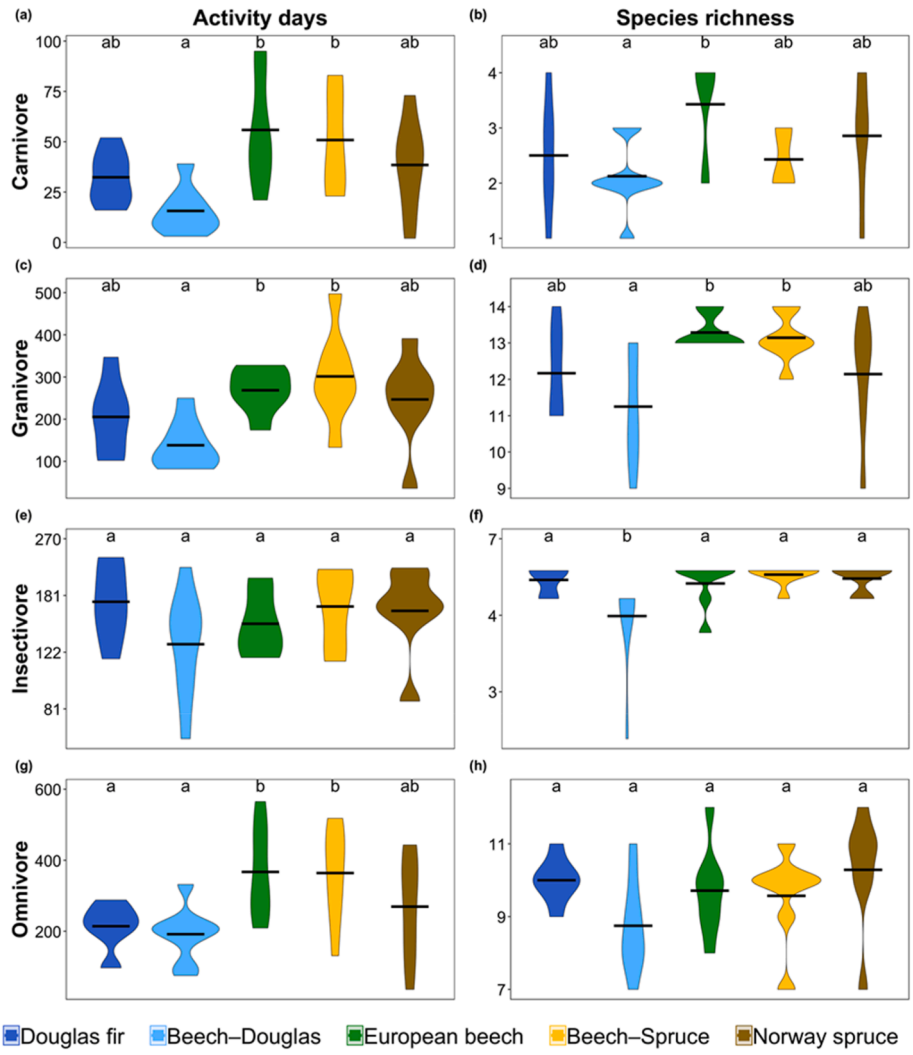

Fig. 3. Activity days and species richness of **(a, b)** carnivores, **(c, d)** granivores, **(e, f)** insectivores, and **(g, h)** omnivores per stand type. Significant differences are marked with lowercase letters, derived from linear mixed-effects models. Coloured areas reflect the data distribution. Black lines are the mean values per plot. *y*-axes of panels are log(x)-transformed to improve model fit. *y*-axes show back-transformed values.

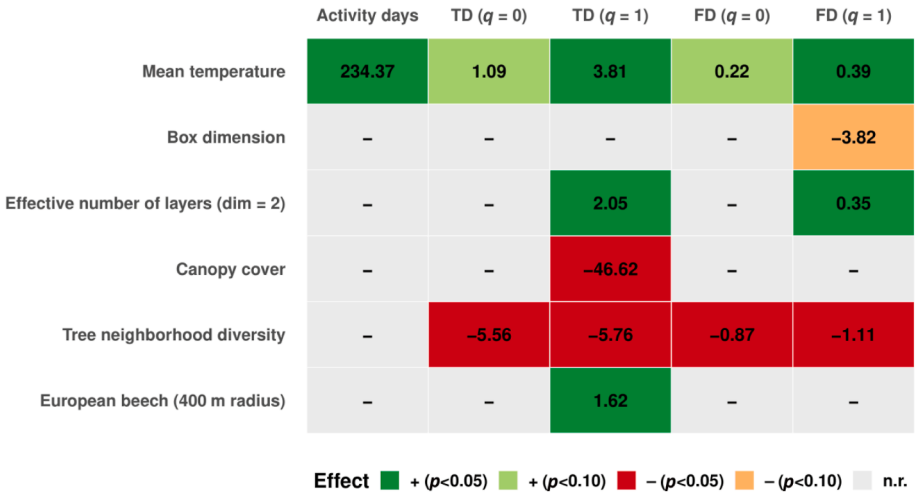

Fig. 4. Relationships between environmental variables and bird activity days and diversity metrics derived from linear mixed-effects models. Plot was nested within site as a random effect, and non-collinear environmental covariates were included as fixed effects. Cells show standardized fixed-effect estimates for each scaled predictor (rows) across bird diversity metrics (columns). Colours indicate direction (green = positive, red/orange = negative); shading indicates significance (dark: $p < 0.05$; light: $p < 0.10$). Cells labelled n. r. indicate predictors not retained in the final (AICc-selected) model.

in stand types with Douglas fir, especially in beech-Douglas fir mixtures (Fig. S5d). When giving more weight to abundant taxa, diversity patterns diverged among stand types for both taxonomic and functional dimensions. For TD, common species ($q = 1$) and dominant species ($q = 2$) were consistently lower in beech-Douglas fir mixtures than in the other stand types (Fig. 5b and c), and Douglas fir monocultures also

showed lower dominant species ($q = 2$) diversity compared to the other stand types (Fig. 5c). Functional diversity exhibited broadly similar patterns, but with a clearly higher FD for $q = 1$ and $q = 2$ in beech-Norway spruce mixtures and beech monocultures than the other stands (Fig. 5e and f). Moreover, Norway spruce monocultures showed higher common and dominant species richness compared to Douglas fir monocultures (Fig. 5b and c). Finally, when pooling stand types into monocultures versus mixtures, extrapolated gamma diversity was higher for monocultures than mixtures for both TD and FD at $q = 1$ and $q = 2$ (Fig. S4).

3.4. Community composition

Bird community composition differed among stand types based on relative activity days (Fig. 6; PERMANOVA, $F_{4,30} = 3.037$, $R^2 = 0.288$, $p = 0.009$). Pairwise PERMANOVA indicated differences between beech monocultures and both Douglas fir and Norway spruce monocultures, as well as between beech-Norway spruce and beech-Douglas fir mixtures (Table S11). In the NMDS ordination, conifer monocultures clustered and remained largely separated from beech and beech-Norway spruce stands. Beech-Douglas fir mixtures occupied an intermediate position (Fig. 6). The dbRDA ordination confirmed this differentiation (Fig. S6 and Table S13). Species positioned closer to conifer monocultures included *Glaucidium passerinum*, *Lophophanes cristatus*, and *Poecile montanus*, whereas *Sitta europea*, *Poecile palustris*, *Coccothraustes coccothraustes*, and *Cyanistes caeruleus* were positioned closer to beech stands (Fig. S5).

Backward stepwise selection retained five environmental predictors in the dbRDA model, which together explained 50.6% of the variation in bird community composition (adjusted $R^2 = 0.41$; $F_{5,27} = 5.54$, $p < 0.001$). All retained predictors had significant marginal effects (Table S13). Mean temperature showed the largest marginal contribution to total community variation (10.7%; $F_{1,27} = 5.86$, $p = 0.010$), followed by Douglas fir cover within a 400-m around the plot (8.2%; $F_{1,27} = 4.50$, $p = 0.017$), mean tree diameter (7.3%; $F_{1,27} = 3.99$, $p = 0.034$), Norway spruce cover within a 400 m around the plot (7.0%; $F_{1,27} = 3.82$, $p = 0.032$), and variation in tree diameter (6.2%; $F_{1,27} = 3.41$, $p = 0.040$). The dbRDA patterns confirmed the NMDS ordination, revealing that community differences among stand types covaried with tree species composition at the landscape scale as well as with forest structure and microclimate characteristics (Tables S12 and S13).

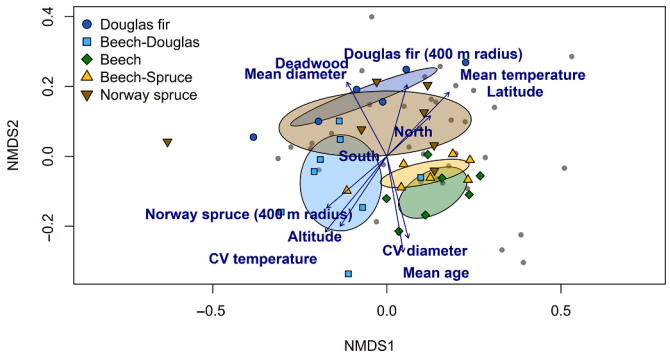

Fig. 6. Nonmetric multidimensional scaling (NMDS) ordination of bird community composition per stand type at plot level. Stress < 0.2. Ellipses show the standard deviation of stand type point scores. Grey dots represent species. Filled symbols represent the study plots and stand types. Environmental variables were fitted post hoc and show significant correlations with axes scores (see Table S12 for details).

The sensitivity analyses excluding *Regulus* sp. produced qualitatively similar results for all response variables (Fig. S7–S9), except for landscape-scale taxonomic diversity, for which the negative association with Douglas fir cover was no longer evident (Fig. S8).

4. Discussion

This study provides the first comprehensive assessment of winter bird responses to forest conversion and mixing strategies involving non-native Douglas fir in temperate Europe, combining PAM with coverage-

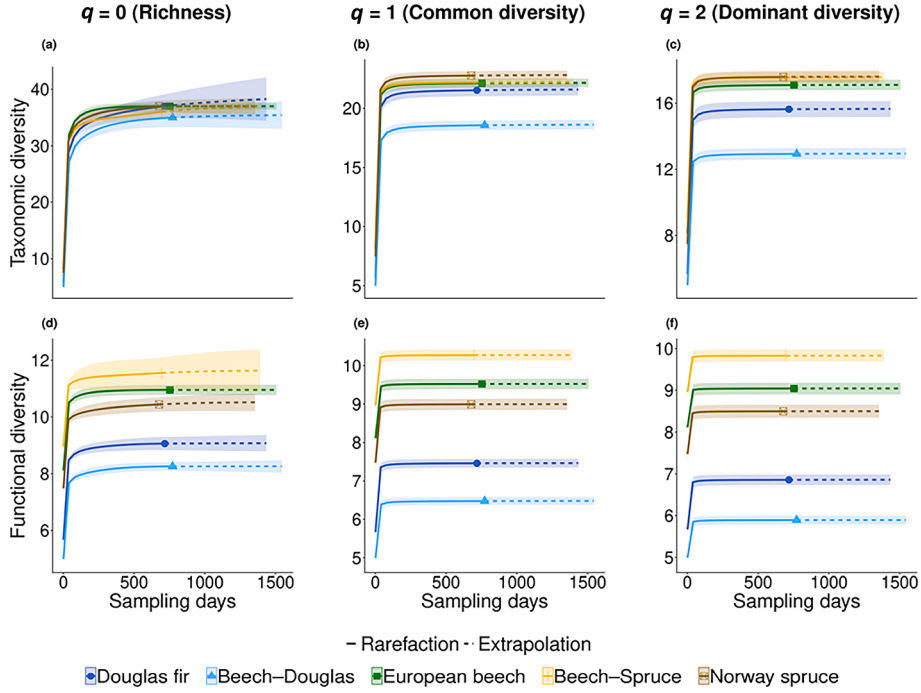

Fig. 5. Incidence-based rarefaction (solid lines) and extrapolation (dashed lines) curves of **(a–c)** taxonomic and **(d–f)** functional diversity of Hill numbers ($q = 0$, 1, and 2) for individual forest stand types across plots. Sampling days correspond to detections pooled within each plot and day (one sample = one sampling day per plot). Shaded areas represent 95% confidence bands.

standardized estimates of TD and FD. Comparisons with breeding-season patterns from the same study sites (Schuldt et al., 2022) suggested that conclusions drawn from summer can only be partially applied to winter. During the breeding season, beech and mixed stands generally support greater bird diversity than conifer monocultures, particularly pure non-native stands (Felton et al., 2021; Hanzelka and Reif, 2016; Schuldt et al., 2022). In contrast, we found that no clear evidence of differences in plot-scale TD at $q = 0$ among stand types, in line with the prediction of our first hypothesis. This seasonal contrast may reflect differences in bird ecology between the breeding and winter periods (Michielsen et al., 2024). Seasonal species turnover via migration may have further contributed to these differences (Felgentreff et al., 2026). Migratory species associated with deciduous forests (e.g., *Phylloscopus collybita*, *Sylvia atricapilla*, *Phylloscopus sibilatrix*) are largely absent in winter, while resident conifer-associated species (e.g., *Regulus* sp., *Periparus ater*) persist (Barbe et al., 2018; Bauer et al., 2005; Schuldt et al., 2022), potentially reducing TD contrasts among stand types.

Clearer contrasts among stand types emerged in activity days, although support for our second hypothesis was limited. Plot-level FD responses were weaker than expected, with stronger stand-type differences emerging at the landscape scale and in the feeding guild analysis. The increased mobility of birds (often in flocks) in winter can blur local-scale differences in TD and FD, while stand-specific conditions can still affect activity day levels and the relative contribution of common species ($q = 1$), potentially through variation in food accessibility (Renner et al., 2012), solar radiation availability (Villén-Pérez et al., 2014), or perceived predation risk (Carr and Lima, 2014). Importantly, some winter-summer differences may also reflect methodological contrasts between studies (Schuldt et al., 2022; point-count abundances in summer vs. PAM-derived indices in winter, and different diversity metrics).

Across these responses, a central result was the scale dependence of stand-type effects on winter bird diversity. Differences in TD and FD, particularly the lower values associated with stands containing Douglas fir, became more evident from plot to landscape scale, where diversity accumulates through between-plot differences (Socolar et al., 2016). This supports our third hypothesis and highlights that biodiversity differences associated with stands containing Douglas fir may be underestimated if judged only from a local plot perspective. Pooled mixtures outperformed pooled monocultures in summer (Schuldt et al., 2022), whereas monocultures performed slightly better in winter, except for beech-Norway spruce mixtures, which showed higher gamma FD than the corresponding monocultures. Mixture outcomes therefore depended on tree-species identity rather than mixture status alone (Pedley et al., 2019; Schuldt et al., 2022; Vélová et al., 2021). Tree-species composition in the surrounding landscape was also associated with bird diversity and community composition. Indeed, beech cover within 400 m was positively associated with TD, whereas Douglas fir and Norway spruce cover contributed to variation in community composition. Winter bird responses thus reflected not only local stand identity but also the surrounding forest mosaic (Baeten et al., 2019; Basile et al., 2021).

This interaction between local stand identity and landscape context was particularly apparent in beech-Douglas fir mixtures, which supported comparatively low activity days, TD, and FD at both plot and landscape scales. Their bird communities were also more similar to those in pure Douglas fir than to those in pure beech stands, indicating that Douglas fir retained community characteristics associated with Douglas fir monocultures potentially through a strong influence on habitat conditions. Previous studies found that beech-Douglas fir mixtures can enhance Douglas fir growth performance relative to pure stands (Thurm and Pretzsch, 2016), and that Douglas fir can overtop beech in mixtures, increasing height stratification (Thurm and Pretzsch, 2016), and altering crown arrangement and microclimatic conditions (Bärmann et al., 2023). Canopy cover (except in Norway spruce monocultures), vertical structural complexity, and microclimatic conditions were similar among stand types in our study and therefore did not explain the observed patterns. Beech-Douglas fir mixtures were also older than Douglas fir monocultures, excluding younger age as an explanation. Because we did not quantify food resources or fine-scale microhabitats, we could not determine whether these local habitat conditions contributed to the observed responses. The low diversity of beech-Douglas fir mixtures may therefore reflect their occurrence within conifer-dominated surroundings, which could limit the potential biodiversity benefits of the local beech admixture (Basile et al., 2021; Renner et al., 2012; Vélová et al., 2021).

Functional diversity was particularly responsive at the landscape scale. Stand types containing Douglas fir supported the lowest effective number of functional groups while TD differences were comparatively smaller for $q = 0$, suggesting that rare functional strategies, or combinations of traits, are less consistently represented in Douglas fir-dominated landscapes, even if local communities are still characterized by similar numbers of species (Bühler et al., 2023). Thus, functional redundancy at the plot scale may buffer FD differences among stand types, but repeated losses across the landscape can reduce communities' functional insurance and resilience (Biggs et al., 2020). Feeding-guild analyses similarly revealed stand-type differences in several activity and richness responses, with beech and beech-Norway spruce stands often supporting higher activity days and species richness than the other stand types (Gossner and Utschick, 2004; Renner et al., 2012).

A key similarity between winter and breeding seasons is that stand type consistently shaped bird communities. Contrary to our fourth, NMDS ordination indicated pronounced turnover of winter birds between beech- and conifer-dominated stands. This aligns with recent findings identifying tree functional groups (coniferous vs. deciduous tree species) as a main driver of bird species composition during winter (Felgentreff et al., 2026). In our study, Norway spruce monocultures showed particularly high species compositional variability. This may be related to differences in canopy structure, as recent local spruce dieback (Schuldt et al., 2020) may have increased compositional variability by creating canopy gaps and greater within-stand structural heterogeneity (Plath and Fischer, 2024; Villén-Pérez et al., 2014), as suggested by the significantly lower canopy cover in Norway spruce monocultures compared to that of other stand types.

The less pronounced negative responses observed in pure Douglas fir stands than expected from breeding-season and previous winter studies (Gossner and Utschick, 2004; Schuldt et al., 2022) suggest that stands containing Douglas fir may less consistently affect winter bird communities than previously assumed. Gossner and Utschick (2004) reported that bird activity was markedly reduced in Douglas fir stands, linked to strongly reduced canopy arthropod densities compared with Norway spruce stands. In our study, the comparatively weak negative response to Douglas fir monocultures may reflect stand-specific characteristics, including their younger age and unexpectedly higher number of deadwood elements, although these variables did not show a significant association with bird activity, diversity, or community composition. One possible explanation is that winter bird communities may be less tightly coupled to arthropod availability if many species broaden their diets when insects are scarce (Díaz-Calafat et al., 2023). Insectivore activity did not differ among stand types, whereas insectivore richness was lower in beech-Douglas fir mixtures, suggesting that insectivore activity was concentrated among fewer species (Bühler et al., 2023). The high contribution of *Regulus* sp. detections may partly explain this pattern, either because the taxon was ecologically dominant or because PAM efficiently records frequently calling species, even after detections are aggregated to daily occurrence (Symes et al., 2022). Acoustic activity should not be interpreted as a direct proxy for abundance, as it is influenced by species-specific calling behavior, habitat-dependent detectability, and weather conditions. The limited changes observed after excluding *Regulus* sp., the most vocally active taxon, suggested that the activity days metric was relatively robust to the influence of highly vocal species. However, it is possible that potential habitat-dependent differences in detection probability among stand types may not be fully accounted for.

Environmental models further indicated associations between winter bird communities, microclimate, and structural complexity, which are partly mediated by stand identity. Mean temperature was positively associated with activity days and with TD and FD at $q = 1$, consistent with reduced thermoregulatory constraints (Brodin et al., 2017). Vertical structure was positively associated with TD and FD ($q = 1$), supporting the role of vertical structural heterogeneity in promoting bird diversity via niche partitioning (Davison et al., 2023). In addition, TD ($q = 1$) was negatively related to canopy cover, contrary to expectations of buffering effects (Díaz-Calafat et al., 2023), possibly because canopy cover—lower in Norway spruce stands compared to the other stand types—reflected stand developmental stage and disturbance history rather than tree species-specific canopy structure, including recent spruce dieback (Schuldt et al., 2020) and the relatively young tree age and high tree densities of Douglas fir monocultures. The negative association between tree neighborhood diversity and all diversity indices suggests that in winter, more heterospecific tree neighborhoods do not automatically translate into greater resource and microhabitat availability.

This study demonstrated the value of PAM, a powerful but still rarely applied approach for winter bird ecology (Darras et al., 2019; Shaw et al., 2021), providing standardized, non-invasive, repeatable sampling under challenging conditions. Future work combining vertically stratified assessment of bird diversity with PAM, in combination with direct measures of food resources (e.g., seed and arthropod availability) and microclimate, along the vertical gradient would help disentangle the proposed mechanisms and clarify when mixtures can buffer the biodiversity limitations of non-native plantations.

5. Conclusions

Our study provides winter-season evidence on bird diversity in Central European production forests, contributing to ongoing debates on the biodiversity impacts of non-native tree species. While our results do not support a categorical exclusion of Douglas fir, they indicate that Douglas fir-associated structural and landscape conditions may reduce winter bird activity and the diversity of common and dominant species. Overall, our results show that tree identity, stand type, and landscape context interact, and that the net biodiversity outcome of mixing depends on how these factors combine. From a management perspective, maintaining broadleaf components at the landscape scale and vertical structural complexity at the stand scale appears essential. In addition, winter communities should be explicitly considered, as breeding-season patterns alone provide an incomplete basis for predicting the overall effects of forest management on biodiversity. Our findings also support current recommendations to limit Douglas fir proportions in mixtures, although optimal mixture ratios and spatial configurations remain important questions for future research.

Ethics statement

This study involved non-invasive passive acoustic monitoring only and did not include the capture, handling, marking, or experimental manipulation of animals. Field access and permission to conduct the study were granted by the responsible forest managers and local forestry authorities at all study sites.

Data availability

Data will be made publicly available upon publication via GRO. data at https://doi.org/10.25625/Q3AJZZ.

CRediT authorship contribution statement

Sara Piccini: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **David Singer:** Conceptualization, Investigation, Methodology, Software, Validation, Writing – review & editing. **Lea Leister:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Micaela Pineda:** Data curation, Investigation, Writing – review & editing. **Alice Penanhoat:** Data curation, Investigation, Methodology, Writing – review & editing. **Dominik Seidel:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. **Martin M. Gossner:** Conceptualization, Methodology, Writing – review & editing. **Andreas Schuldt:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Sara Piccini reports financial support was provided by German Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2026.100519.

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